

THE TUBEROUS EPIPHYTES OF THE RUBIACEAE 4: A REVISION OF SQUAMELLARIA

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SUMMARY

Squamellaria Becc. is revised to include three species, one of which new, and one existing species is reduced. The genus is endemic to Fiji.

Confined to the eastern Fijian Islands, *Squamellaria*, with just three species, is the smallest genus of the Hydnophytinae (Huxley & Jebb, 1991). Beccari (1886) originally separated this genus from *Hydnophytum* Jack, to which it is most closely related, on account of the four fringed plates (squamellae) inside the corolla tube, the capitate stigma, and the curved pyrenes with short embryos and bony endosperm.

Study of the tuber has revealed a remarkably complex cavity structure, which further strengthens the taxonomic 'moat' between this genus and *Hydnophytum*. The tuber of all *Squamellaria* species has the same basic structure: it is cylindrical, with rings of regularly spaced, rimmed holes, encircling the tuber. Between these rings of holes the tuber wall, of *S. thekii* in particular, swells outwards, such that the tuber appears crenate in outline. A mature tuber contains several, essentially similar cavities. Each cavity is produced sequentially at the tuber apex, between the last formed cavity and the base of the stem. Several distinct chamber types are recognised (Jebb, 1985). Each cavity has a superficial planar 'Girdle Chamber' (fig. 1). This chamber all but encircles the tuber, and gives rise apically to a ring of entrance holes. The Girdle Chambers interconnect to older cavities along their basal edge, and to younger cavities along their apical edge. Ventrally they are blind-ended and densely warted, while dorsally and basally they give rise to numerous 'Superficial Smooth Walled Chambers' which overlie the Girdle Chamber of the previous cavity. From its inner wall the Girdle Chamber gives rise to 'Deep-lying Smooth Walled Tunnels' (fig. 1).

Squamellaria also differs from the rest of the Hydnophytinae in that the stems do not arise only at the tuber apex. In *S. imberbis* the stems arise from the apical $\frac{1}{2}$ to $\frac{1}{3}$ of the tuber, most stems being clustered close to the apex (fig. 2). The stems are slender and branched. In *S. major* the stems are more remote from one another, one stem apparently arising between each ring of entrance holes (fig. 3); thus each stem appears to be associated with the formation of a new cavity. In this species the stems are thickened and unbranched.

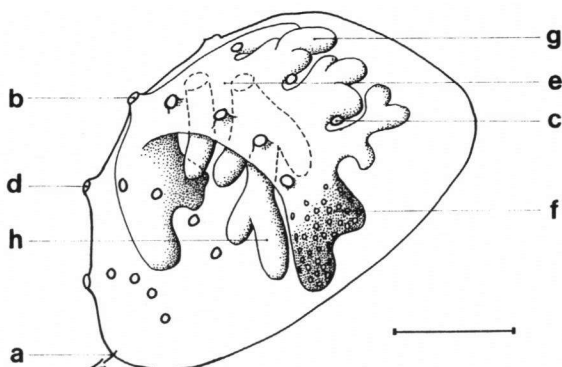


Fig. 1. Schematic diagram of a single cavity within a tuber of *Squamellaria imberbis* (A. Gray) Becc. a. Tuber apex; b. entrance hole; c. entrance hole of preceding cavity; d. entrance hole of later cavity; e. girdle chamber; f. warted extremities of girdle chamber; g. superficial smooth walled chamber; h. deep lying smooth walled tunnel. Scale bar = 10 cm. Drawn by Rosemary Wise.

The stigma and anthers are exserted. The stigma is capitate and finely fringed along the lower edge. None of the species shows heterostyly, and the large capitate stigma, lying immediately above the anthers, suggests a presenter mechanism. The long, often curved corolla tube suggests moth pollination. No observations of nocturnal opening or scent production have been made. It is interesting that solitary sessile inflorescences and relatively large (110–163 μm) four-colpate pollen, as found in *Squamellaria*, also occur in the Fijian species of *Hydnophytum*, (pollen 80–130 μm across).

Beccari's original two species are here reduced to one. Smith (1967) described a new species and reported that all species had a chambered tuber inhabited by ants. The present author collected all the species in 1985 and was able to study the tuber and flower structure. All material is cited, marked n.v. if not seen. The figure in brackets after *Flower* in the descriptions is the number of flowers dissected.

SQUAMELLARIA

Squamellaria Becc., *Malesia* 2 (1886) 228; K. Schumann in Engler & Prantl, *Nat. Pflanzenfam.* IV, 4 (1891) 123; A.C. Smith, *J. Arn. Arbor.* 36 (1955) 289; S. Darwin, *Allertonia* 2 (1979) 35; A.C. Smith, *Fl. Vit. Nova* 4 (1988) 245. — Type species: *S. imberbis* (A. Gray) Becc. [*Myrmecodia imberbis* A. Gray, *Proc. Am. Acad. Arts & Sci.* 4 (1858) 42].

Epiphytes. *Tuber* cylindrical, ovoid to oblong. Spines simple, slender, mostly flexible, scattered, sometimes more numerous around entrance holes. Surface smooth, blackish, occasionally with numerous white tubercles to 2 mm in diameter. Entrance holes in discrete regular rings around the tuber, to 4 mm in diameter, conical, or with prominent, grey or white, spine-fringed rims. Pores and ridges absent. *Stems* few to numerous, scattered or arising from one or more basal stock(s); subherbaceous to woody, branching or not, to 50 cm long, 1.5 cm thick, rounded, smooth, mostly

lacking spines. *Leaves* clustered or remote. Lamina $3.5 \times 1.5 - 17 \times 6.5$ cm, cordate, rhomboid-lanceolate or obovate, thin to thick, fleshy. Stipules thin, papery, to 3.5 mm, splitting opposite the petiole at first, soon tearing between the petioles. *Inflorescence* solitary, laterally displaced in axil, sessile at first, becoming pedunculate with age. Bracts inconspicuous. *Flowers* homostylous. Calyx 2–6 mm, entire or with 4 triangular lobes. Corolla commonly distorted, curving sharply at base or towards middle, quadrangular or inflated, white throughout, or with green or red markings on the corolla lobes, pubescent without; 4 barbate plates (squamules) towards base of tube, occluding lumen. Anthers 4–8 mm, exserted. Pollen 3–5-colpate, 110–163 μ m in diameter; colpi almost as long as the grain, sometimes partially occluded by pollen wall extensions; walls 9–14 μ m; reticulation open, coarse, 6–30 μ m; vesicles absent. Stigma capitate, with $4 \pm$ indistinct lobes, depressed at apex, recurved and sometimes fringed at margin. *Fruit* fleshy or siccate, markedly tetragonal or ovoid, orange-red; calyx remains prominent. Pyrenes 4, more or less hooked, sometimes with a ridge on the abaxial surface.

Ecology – High or low in host tree, in open to dense forest from 200–2000 m. All species are inhabited by *Iridomyrmex* ants.

KEY TO THE SPECIES OF *SQUAMELLARIA*

- 1a. Petiole 0.4–3.5 cm, lamina lanceolate to rhomboid, thin, with a flat margin. Stems slender, not thickened towards their apex 1. *S. imberbis*
- b. Petiole very short, to 0.5 cm, lamina obovate or ovate to cordate, thick and fleshy, margin irregularly undulate. Stems markedly thickened towards their apices 2
- 2a. Tuber apex blunt. Stems arising individually, to 1.5 cm in diameter near their apices. Leaves obovate, the apex rounded and sometimes minutely acuminate. Corolla lobes parallel-sided in middle, with red and green markings
2. *S. major*
- b. Tuber apex tapered. Stems arising in clusters, to 0.8 cm in diameter near their apices. Leaves ovate to cordate, apex acute. Corolla lobes obovate, pale green
3. *S. thekii*

1. *Squamellaria imberbis* (A. Gray) Becc. – Fig. 2.

Squamellaria imberbis (A. Gray) Becc., *Malesia* 2 (1886) 228, t. 46, figs. 1–12; A.C. Smith, J. Arn. Arbor. 36 (1955) 289; J.W. Parham, Pl. Fiji Isl. (1964) 209, ed. 2 (1972) 293; A.C. Smith, Fl. Vit. Nov. 4 (1988) 247. — *Myrmecodia imberbis* A. Gray, Proc. Am. Acad. Arts & Sci. 4 (1858) 42; B.C. Seemann, Fl. Vit. (1866) 138. — *Myrmecodia inermis* A. Gray ex Hook. f. in Benth. & Hook. f., Gen. Pl. 2 sphalm. (1873) 132. — *Hydnophytum imberbe* Benth. & Hook. f. ex Drake, Ill. Fl. Ins. Mar. Pac. (1890) 200. — Type: Fiji, U.S. Expl. Exped. U.S. 62266 (holotype US; isotype K).

Squamellaria wilsonii (Horne ex Baker) Becc., *Malesia* 2 (1886) 229, t. 46, figs. 13–21; A.C. Smith, J. Arn. Arbor. 36 (1955) 289; J.W. Parham, Pl. Fiji Isl. (1964) 209, ed. 2 (1972) 293, sphalm. *wilsonii*; S. Darwin, Allertonia 2 (1979) 35, fig. 3D; A.C. Smith, Fl. Vit. Nov. 4 (1988) 247, figs. 9A–D & 13a. — *Hydnophytum wilsonii* Horne, A Year in Fiji (1881) 263, nom. nud.; Horne ex Baker, J. Linn. Soc. Bot. 20 (1883) 365; Drake, Ill. Fl. Ins. Mar. Pac. (1890) 200. — Type: Fiji, Horne 1139 (holotype K).

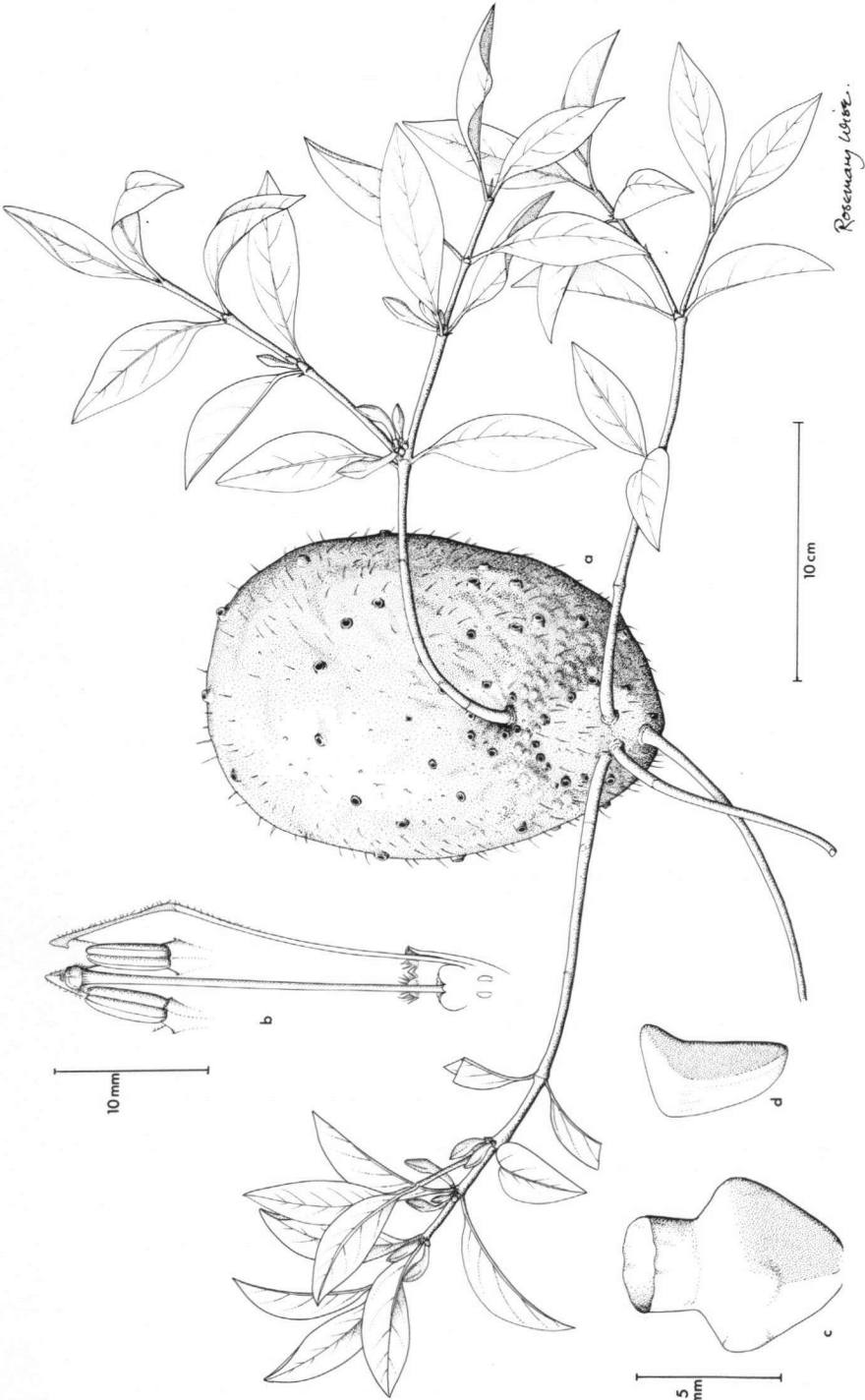


Fig. 2. *Squamellaria imberbis* (A. Gray) Becc. a. Whole plant; b. flower; c. fruit; d. pyrene (all Jebb 467). Drawn by Rosemary Wise.

Tuber growing horizontally from host, regularly oblong to subovoid nearly horizontal below, swollen above, more or less bluntly hemispherical from the side, elliptic in longitudinal section, to 30 cm long, 18 cm high, and 12 cm wide; surface glossy to matt black. Spines to 2 cm mounted on small protrusions. Entrance holes conical, 0.6 cm in diameter, more numerous on upper surface; rims to 0.4 cm high, green to grey. *Stems* several, branching, to 50 × 0.6 cm, pendent to upcurving; mostly arising on the apical part of the tuber, less remote towards the apex. Internodes up to 4 cm long when sterile. Spines only present very close to tuber, rare elsewhere on stem. *Leaves*. Lamina 4.5 × 1.5 – 8.5 × 3.5 cm, lanceolate to rhomboid, apex acute, base tapering to petiole, mid green. Midrib prominent below, pale green to pinkish; veins c. 5–7. Petiole 0.4 to 3.5 cm, pale green to pink. Stipules to 3.5 mm long, apiculate, with a small central process to 0.15 cm, caducous. *Inflorescence* sessile to pedunculate, to 0.6 cm long and 0.3 cm thick. Bracts to 0.1 cm. *Flowers* [11]. Calyx 2–3 mm, entire or finely mucronate, pubescent. Corolla white, quadrangular, to 32 mm, pubescent without, especially on corolla lobes, bud densely so, rarely glabrous. Corolla tube more or less recurved at base, tapering to base. Lobes triangular, 6.5 mm long, acute, tetragonal in bud. Anthers 4–5 mm long, blue-black; filaments to 2 mm wide. Pollen (3–)4(–5)-colpate, 110–152 (134.5) µm in diameter; colpi with a slightly thickened border, about as long as the height of the grain; walls 9–10 µm thick, the inner wall to 3 µm, the outer layer regularly reticulate, these lumina 6–16 µm across, the foot layer within the lumina with minute perforations. Stigma immediately above anthers, with 4 indistinct lobes and a fringe of short hairs below. *Fruit* turbinate, strongly quadrangular, not fleshy, to 7 mm including calyx. Pyrenes 5 mm long, tightly appressed in fruit, strongly curved.

Ecology – Altitude 300–700 m. Not solitary, several specimens usually present in a given tree.

Notes – The regular, oblong, and slightly compressed tuber, with fine-rimmed unarmed entrance holes is diagnostic. The thin, lanceolate leaf and flowers also isolate this species from the remainder of the genus.

Squamellaria wilsonii was formerly distinguished by its shorter corolla, lobes longer relative to the tube, stamens longer than filaments, fruit more globose, pyrenes less hooked, and leaves more acute and gradually attenuate (Beccari, 1886), and longer calyx limb (Smith, 1988). In the light of further collections and study of fresh material, these differences have proved insignificant, or due to developmental stages, or the vagaries of drying.

Collections – FIJI ISLANDS. Vanua Levu. SE 16° 30' 179° 19', Thakaundrove, Yanawai River region, Mt Kasi, *Smith 1787* (BO, GH, K, UC). 18° 04' 178° 25' Korotini Range, near new road from Savusavu to Lambasa, *Jebb 467* (BISH, K), 468 (LAE, SUVA), 469 (BULOLO, K, SUVA), 470 (A, BRI, CANB, SUVA), 471 (BISH, FHO, K, SUVA), 472 (SUVA). Crest of Korotini Range, between Navitho Pass and Mt Ndelaikoro, *Smith 564* (n.v.). — Taveuni. 16° 48' 179° 58' Western slopes between Somosomo and Wairiki, *Smith 750* (BO, H, UC). Above Qacavulo Estate, A.C.S., J.W.P., P.B.T., D.K. 16935 (BRI). Slopes of Mt Manuka, east of Wairiki, *Smith 8191* (GH, L, UC), 8326 (K, L, UC). 16° 50' 180° 00', on road to Devoeux Peak, *Jebb 479* (BISH, K, SUVA), 480 (BISH, SUVA), 481 (BISH, K, SUVA), 482 (LAE, SUVA, UPNG). Above Nggathavula Estate, *DA 16935* (n.v.). Nggarawalu, Freehold *DA 11901* (n.v.). Forest Creek, *Horne 1139* (K) (type of *S. wilsonii*). — Locality uncertain. *Seemann s.n.* (K, P). Mathuata Prov., U.S. *Expl. Exped. US 62266* (type).

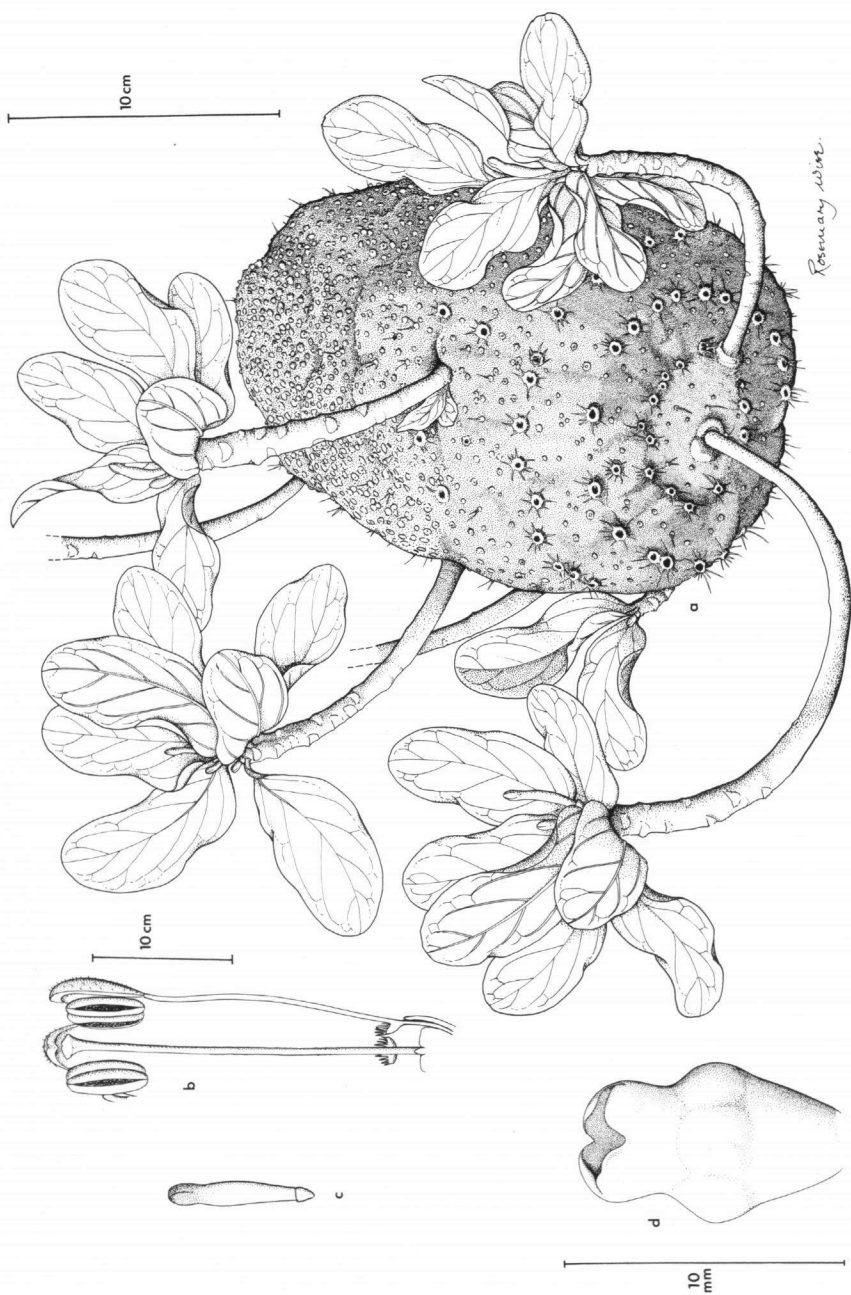


Fig. 3. *Squamellaria major* A.C. Smith. a. Whole plant; b. flower; c. bud; d. fruit (a: Jebb 475; b-d: Jebb 483). Drawn by Rosemary Wise.

2. *Squamellaria major* A.C. Smith – Fig. 3.

Squamellaria major A.C. Smith, Cont. U.S. Natl. Herb. 37 (1967) 90; J.W. Parham, Pl. Fiji Isl. ed. 2 (1972) 293; A.C. Smith, Fl. Vit. Nov. 4 (1988) 247. — Type: Fiji, *Smith 8323* = *US 2191043* (holotype US; isotype BISH, K, L, US).

Tuber subpendent, cylindrical, obovate, apex blunt to 24(–40) × 17 cm. Surface with small white tubercles, black. Spines stiff to flexible, to 1.5 cm long. Entrance holes 1 cm in diameter with a thickened, spine-topped, white rim to 0.3 cm across. *Stems* several, apparently arising from immediately within each ring of entrance holes, unbranched, scattered, to 20 × 1.5 cm, fleshy, surface smooth, grey; internodes 0.5–1.5 cm, shortest and thickest towards apex. *Leaves* clustered at apices. Lamina obovate to broadly oblong-elliptic, 8 × 4.5 – 17 × 6.5 cm; apex rounded, apiculate or not, base abruptly narrowed, blunt or cordate, drying thin, yellowish green above and below. Midrib narrowing abruptly at each venation branch, often bifurcate near apex. Lateral veins prominent above and below. Margin irregularly undulate, white. Petiole 0.3 to 0.5 cm. *Inflorescence* sessile. *Flowers* [3] to 35 mm. Calyx cup-like, narrowed at margin, with 4 gentle undulations, to 5 mm long. Corolla recurved, white, lobes green with a pale red or pink patch at the centre, to 31 mm long; lobes to 7 mm, pubescent, rounded in bud, sides parallel when mature. Tube inflated towards middle, to 7 mm in diameter, narrowing towards apex, and then widening slightly at mouth; barbate scales 2 mm above the disc. Anthers 5–6 mm; filaments to 2.5 mm. Pollen 4- or 5-colpate, 125–163 (140) µm in diameter; colpi edges barely thickened, colpi to 14 µm across, about as long as the height of the grain, the colpi being more or less occluded by a number of fine outgrowths of the pollen grain wall, which arise from both edges of the colpus and interdigitate; walls to 12 µm thick, the inner wall to 6 µm, the outer wall irregularly reticulate, these lumina 9–30 µm, the foot layer within the lumina with numerous small outgrowths. Stigma square in section with 4 mounds, exerted above anthers. *Fruit* to 1 cm, fleshy, quadrangular below, with prominent calyx to 3 mm. Pyrenes hooked, to 5.5 × 3 mm.

Ecology – Growing on trunks or large limbs of trees in closed forest at 300–400 m. Often solitary or few in number.

Note – The leaves of this species always appear chlorotic and diseased. Examination of fresh tuber material reveals that the small white tubercles that cover the outside of the tuber have fungal hyphae in them.

Collections – FIJI ISLANDS. Taveuni. SE 16° 50' 179° 59' Slopes of Mt Manuka, east of Wariki, *Smith 8323* (type). 16° 50' 180° 00', on road to Devoeux Peak, *Jebb 475* (FHO, SUVA), *476* (BISH, SUVA), *483* (SUVA).

3. *Squamellaria thekii* Jebb, *spec. nov.* – Fig. 4.

Tuber fusiforme, tumidum inter annulos foraminum, qua foramina margine incrassato. Caules paullo incrassati apicem versus, ad 8 mm diametro, ramosi, ab tubere uno fasciculo vel pluribus orientes. Folia fasciculata, obovata usque ovata, apice acuto usque rotundo, basi obtuso, carnosae, margine corrugata. Calyx 4-dentatus. Corolla alba, lobi tumidi in alabastro, obovati in maturitate. Fructus ovoideus, calyce manifeste coronatus. — Typus: Fiji, *Jebb 477* (holotypus SUVA; isotypi BISH, K; cotypus *Jebb 478*, SUVA).

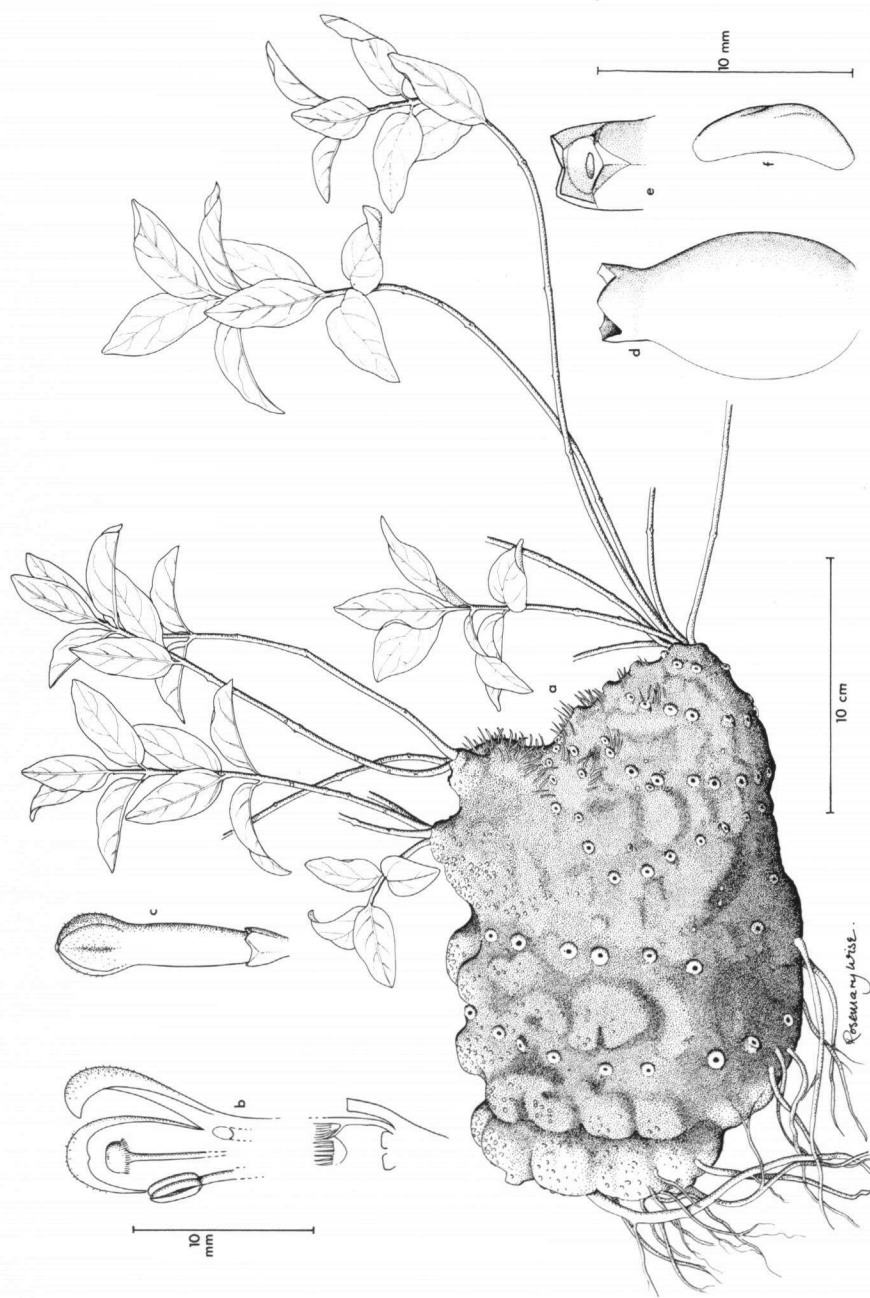


Fig. 4. *Squamellaria thekijebbi*. a. Whole plant; b. flower; c. bud; d. fruit; e. calyx and disc at fruit apex; f. pyrene (all Jebb 477). Drawn by Rosemary Wise.

Tuber subpendent, regular, cylindrical-fusiform, tapering to base and apex, abruptly swollen between the rings of entrance holes, to 27 cm long, 9–15 cm wide; surface rough, with numerous small protuberances, some giving rise to hair-like spines to 1.5 cm long, dark brown to black. Entrance holes numerous, in rings 1 to 5 cm apart; prominent, with a thickened rim to 0.2 cm, the inner edge abrupt, to 0.8 cm across. *Stems* several, arising from one to few scattered clusters, unbranched, to 36 × 0.8 cm. Internodes 0.3–3 cm. *Leaves* clustered at apex. Lamina cordate to ovate rhomboid, apex acute, base blunt to cordate, margin crinkled. Petiole up to 0.2 cm. Stipules rounded, to less than 0.1 cm long, caducous. *Inflorescence* sessile. Bracts papery, to 0.2 cm. *Flowers* [2] to 36 mm. Calyx to 5 mm, fleshy, quadrangular, 4-dentate, abruptly flattened at margin. Corolla white, minutely pubescent on lobes, to 31 mm. Corolla tube swelling towards middle, to 6 mm in diameter, gently recurved. Lobes obovate, blunt, to 8 mm, with a deep groove on the outer surface, more or less orbicular in bud, scales 2 mm above the disc. Anthers to 3.5 mm, filaments to 3 mm. Pollen 4 colpate, 150–163 µm; colpi to 19 µm across, edges thickened; walls to 14 µm, the inner wall to 4.5 µm, the outer wall irregularly reticulate, these lumina 9–22 µm, round the foot layer within the lumina smooth. Stigma above anthers, to 2 mm in diameter, rounded, margin reflexed and fimbriate. *Fruit* to 10 mm, ovoid, fleshy. Pyrenes to 6.5 × 3 mm, slightly recurved, with a prominent abaxial keel.

Ecology – A low level epiphyte, growing on trunks of trees in forest at 300–400 m.

Notes – A little known species, only collected once, and apparently not as common as the two species with which it is sympatric. Its stem and leaf characters suggest an intermediate position between the other species, but flower characters indicate its specific status. The distribution of stems on the tuber surface is peculiar to this species; in *S. major* and *S. imberbis* the stems are scattered, while here they arise in clusters at the apex of the tuber and elsewhere.

The specific epithet derives from the Fijian name 'theke theke nkau' for ant-plants, meaning 'testicles of the trees'.

Collections. FIJI ISLANDS. Taveuni. SE 16° 50' 180° 00', Taveuni road to Devoeux Peak, *Jebb* 477 (type), 478 (cotype).

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